THE DISTRIBUTION OF DIOSPYROS VIRGINIANA L.* HARRY R. SKALLERUP**

While the factors responsible for the present distribution of D. virginiana are in themselves not unique, the study of the literature pertaining to the native persimmon is particularly rewarding. Because the persimmon is both a fruit and forest tree the information obtained is increased two-fold. The combination of botanical, horticultural, and dendrological data answers some of the questions in regard to the determination and interpretation of the many aspects of its life phenomena. An attempt will be made here to present the factors affecting the macro- and micro-distribution of D. virginiana and to review and supplement certain aspects of the literature relating to them. The genus Diospyros has a fossil record extending to the Mid-Cretaceous Era, and is represented by leaves, wood, calices, and even fossilized fruit, each having been reported from various locations throughout the world. Species evidently grew in Greenland, Siberia, Canada, northern Japan, Alaska, the British Isles, and in North Africa and Arabia (Berry, 1923). Although no major geographic region of the United States is without one or more fossil representatives of this genus, only one, based upon wood from a Pleistocene deposit in Louisiana, has been designated D. virginiana (La Motte, 1952). Yet it is reasonable to assume, in the light of leaf variation evident within the extant species, that perhaps a few others of the North American forms based on leaf remains and present as far back as the Cretaceous (Berry, 1923) may also be D. virginiana. Indeed, the present distribution pattern of D. virginiana indicates a very long history. In common with other plants of chiefly tropical affinity, it appears to have been dispersed throughout eastern United States from ancient centers in the Appalachian-Ozark highlands (Fernald, 1931).

Diospyros virginiana is now known only from the United States, and occurs within the area depicted in fig. 1. Each dot represents a county from which a collection has been reported. The apparent low density of collections in the Southeast can best be accounted for by a lack of records from this area. Thus, although only a few collections are represented from Mississippi, Alabama, and Louisiana, floras of these states list D. virginiana as occurring throughout the area. Moreover, a survey of the commercial stands of persimmon timber in the United States showed these states to be especially well represented (Fletcher, 1915). The critical collections at the periphery of its range are likely to define its extent fairly well, since specimens representing the rare species and new range extension are collected with a frequency disproportionate to their occurrence in the natural vegetation.

*This paper is a portion of a monograph on the native persimmon, presented as a master's thesis in the Henry Shaw School of Botany of Washington University. Most of the bibliography of the original thesis has been retained since it includes some references not generally available. **University of Minnesota. Formerly Graduate Research Assistant, Missouri Botanical Garden.

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Fig. 1. Range of Diospyros virginiana L. Glacial and climatic boundaries drawn after Flint (1945) and Kincer (1922, 1928), respectively.

The study of the distribution of a tree such as *D. virginiana* has its disadvantages as well as its advantages. Specimens may be reported or collected from trees introduced outside the natural range, and although the trees may be hardy in these sites they could not have survived in nature as seedlings. Also, reports of non-fruiting specimens, particularly in the older horticultural accounts which ascribe non-fruiting to cold temperatures, may be erroneous due to the fact that *D. virginiana* is dioecious and some of the trees in question may be staminate.

Diospyros virginiana is found growing widely in areas of older glaciation (the Nebraskan, Kansan, and Illinoisan) and in the unglaciated area of the South. In the north and west of the older glaciated area D. virginiana appears to be limited by temperature and rainfall, respectively. Few specimens were found north of the 25° F. February isotherm as determined by Kincer (1928)¹. Inasmuch as individual trees transplanted north of the 25° isotherm are able to survive and bear fruit, it seems that the photoperiod is not a factor in flower formation, and therefore does not limit its distribution (Naudin, 1880; Harrington, 1900; Trabut, 1926; Baldwin and Culp, 1941). It is possible that seedlings in the wild are unable to withstand the cold and to become established in such areas. This is supported by the report of Aikman and Boyd (1941) that persimmon trees planted for soil con-

¹Of the series of maps prepared by Kincer (1928), February represents the coldest winter month for a period of 20 or more years.

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servation purposes in southeastern Iowa (at the northwest limit of the range) needed a protected site if they were to survive.

In determining which factors might account for the western limits of the species, two possibilities appear: both the line of 30 inches of annual precipitation and an increase of 1000 feet in elevation running northward from the Edwards Plateau coincide fairly well with the distribution of D. virginiana. Since the persimmon is found commonly in the southern Appalachians (Eddy, 1927), it is more probable that the rainfall is limiting. (In the more northern mountains of Pennsylvania and West Virginia, persimmon is reported to be more rare than in the lowlands-letters from J. A. Small, E. L. Core-but here the lower winter temperatures and high elevations are probably responsible.) While it is not known at which phase of its growth the moisture requirement may be critical for D. virginiana, in other fruit trees it has been found that an annual precipitation of at least 30 inches is required by mature individuals (Magness and Traub, 1941). While temperature and rainfall thus appear to limit the greater part of the range of D. virginiana, there is a conspicuous absence of specimens from the area of the last or Wisconsin glaciation within the compass of the 25° isotherm. That this area does not differ significantly in climate fails to explain the absence of D. virginiana in the later glaciated region. Berry (1923) states that during Pleistocene times the native persimmon retreated far to the south of the ice front, only to spread north again in the "wake of the ice sheet." With regard for the dangers in assuming that post-glacial expansion is still going on (Deevey, 1949), it would appear that D. virginiana had advanced into the glaciated area, only alternately to withdraw and advance in response to the Wisconsin glaciation, so that now it occupies the northern boundary of the older glaciation (where it is not limited by low temperatures) and has made but slight advances into Indiana, New Jersey, and Connecticut, the areas of the more recent glaciation. The isolated specimens in Indiana, Ohio, and New York (fig. 1) probably represent collections from cultivated trees, as does a specimen from Massachusetts (not shown on map-letter, R. Rollins, 1953).

Baldwin and Culp in 1941 made a cytological study of persimmon from selected stations throughout the range and found that two chromosome races are present: 2n = 60 and 2n = 90. Considering other members of the genus (Table I) it appears that the basic number of chromosomes is 15; accordingly the races of D. virginiana are regarded by Baldwin and Culp as tetraploid and hexaploid. Their relative distribution is interesting: the 60-chromosome race has a continuous distribution in the central and southeastern parts of the range, while the 90-chromosome race occupies a peripheral position throughout the rest of the range. Several additional counts were made in this study. Collections of seeds gathered in St. Louis, Franklin, and Bollinger counties in Missouri, and from Washington County, Arkansas, were grown in the experimental greenhouse at the Missouri Botanical Garden. Chromosome counts made from aceto-lacmoid root tip squashes

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TABLE I

SUMMARY OF KNOWN CHROMOSOME NUMBERS IN DIOSPYROS*

Species	2 n	Source
D. discolor	30	Namikawa, Sisa, and Asai (1932)
D. texana	30	Baldwin and Culp (1941)
D. lotus	30	Namikawa and Higashi (1928)
D. kaki	90	Namikawa and Higashi (1928)
D. virginiana	60, 90	Baldwin and Culp (1941)

*After Baldwin and Culp, 1941.

showed these to have 90 chromosomes-the number reported by Baldwin and Culp in Crawford County, Kans., and Jasper County, Mo. While it would be premature to draw conclusions as to the meaning of the chromosome races in this species, it is of interest to note that the 60-chromosome individuals are found in and about the ancient eastern center of the species. The occurrence of higher polyploids on the periphery of the range is subject to two interpretations: (1) that they are autopolyploid derivatives which have been able to colonize areas not so accessible to the lower polyploid (Cain, 1944; Stebbins, 1950); (2) that the 90chromosome race is actually of hybrid origin (with an extinct species or race) and is spreading eastward along the northern boundary of tetraploid D. virginiana. In either case, studies of both the morphology and cytology of plants of known

chromosome number will be required before the question can be answered even tentatively.

In the course of horticultural practice D. virginiana has been introduced into climates outside of its natural range with varying degrees of success. It had been introduced into England before 1629. Parkinson's 'Paradisi in Sole Paradisus Terrestris' gives the first account of cultivated persimmon trees (Lotus virginiana). One specimen given to George III by the Duke of Argyle (ca. 1790) and grown in the old Kew Arboretum was of considerable dimensions in 1895. At that time it was "apparently as contented [there] as in its native habitat" (For. and Gard., 1895). Diospyros virginiana has also been grown successfully in British Guiana (Hiern, 1873); it fruits regularly in the warmer European climates, although it is irregular in more severe climes where it has been reported to withstand temperatures as low as -25° C. (Naudin, 1880; Trabut, 1926).

FACTORS AFFECTING LOCAL DISTRIBUTION

Although the persimmon is frequently cited in the literature as a pioneer species -a tree that is among the first to grow in almost any situation-a survey of the flora growing spontaneously within the present city limits of St. Louis failed to show any persimmon trees growing in those abandoned places where a "pioneer" would be expected. That persimmons did grow in the area now incorporated as St. Louis proper is borne out by a few, but reliable, references. One of the most

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Fig. 2. Map showing occurrence of *D. virginiana* in the St. Louis area. Black dots represent sites where it was found closest to the city; circles represent apparently favorable sites where it did not occur.

interesting is the narrative by Elizabeth Kennerly Russell, 'Persimmon Hill'. Although written in the style of a saga, its title refers to the actual Kennerly mansion, *Côte Plaquemine*, built in 1832 on a hilly tract of land "five miles northwest of town . . . where Taylor and Kennerly Avenues cross today," and named for the persimmon trees commanding the site (Russell, 1948). Prior to this time the land outlying St. Louis that was not upland forest had been kept in prairie by the Indians who annually burned the vegetation in order to flush out game. By 1836, the prairies had practically disappeared, due to the cessation of the autumnal fires and were succeeded by young forests (Beilmann and Brenner, 1951). Nicholas Riehl, collecting in 1838, gathered persimmon specimens from the "fôrets" of St. Louis; while a visiting farmer, Patrick Shirreff, tasted his first persimmon upon travelling Old St. Charles Road, only to mention its disagreeable taste in a letter written home, dated 1835 (Stevens, 1906). Coincidental in time and place with references to the flora are necessarily those to the birds and animals of the region about which William Kennerly reminisces ". . . we learned the ways

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TABLE II

Road	Sites where D. virginiana was found (represented by black dots, fig. 2)	Sites where D. virginiana was not found (represented by circles, fig. 2)
I. U.S. 61	 (1) Clone, on top of slope at edge of old field with 5, 7* (2) Individuals in grove with 2, 4, 8 	Mixed oak association
II. Telegraph Road	Scattered, on top of ravine, s.w. side in mixed oak woods	Flood plain of Mississippi River

III. U.S. 66	(1) Clone, same as I (1). (2) Scat- tered, in grove with Pinus echinala, 1, 2, and 6	Mixed oak association
IV. U.S. 50	Clone, on slope of old field at edge of grove of Ulmus	Along River des Peres
V. Clayton Road	Scattered, in stand of 1, 2, 3, 4, 8, and Cornus sp.	Brier thicket in recently cleared field
VI. Alternate U.S. 40	 (1) Clone, slope of old field, with 5, 7, Andropogon virginicus, Aster sp. (2) Individual in mixed oak association 	 (1) Flood plain of Missouri River at St. Charles (2) Mixed oak association
VII. Old Florissant	Scattered, along ditch with 4, 5, 7, Rhus glabra, Populus deltoides. Also, specimen of D. virginiana var. pubes- cens found here	Mixed oak association
VIII. Missouri 99	Scattered, side of road, with 2, 4,	Dense grove of Ulmus at edge of

IX. Missouri 109 (not on map) 6, 8, Rhus glabra, Prunus sp.

Scattered, on glade with Bumelia lanuginosa, Cercis canadensis cultivated field

*1. Acer Negundo
2. Celtis occidentalis
3. Platanus occidentalis
4. Quercus sp.

Rubus sp.
 Sassafras albidum
 Symphoricarpos orbiculatus
 Ulmus americana

of animal life in the woods and meadows . . . we could read the small dainty hoofprints of the deer as well as the bobcat's heavier tread . . ." (Russell, 1948). Wild turkey, deer and abounding game were also written of by Flagg in 1836 (Thwaites, 1896–1901; see also Beilmann and Brenner, 1951, for a more complete account). However, with the expansion of the city, persimmon became scarce within its limits. In 1911 the Engelmann Botanical Club listed *D. virginiana* occurring in St. Louis proper only in such floral sanctuaries as Missouri Botanical Garden and in Tower Grove and Forest parks (Engelmann Bot. Club, 1911).²

²Unfortunately the origin of these trees, like plants in many parks and botanical gardens, is speculative. Among the trees in the nursery of Tower Grove Park in 1871, fifty were listed as being persimmons (Shaw, 1871). Henry Shaw, in addition to purchasing the Riehl collection of herbarium specimens, also bought the first trees planted in his Garden from the Riehl Nursery (Spaulding, 1909).

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Ironically, a year later persimmon was recommended as a native tree suitable for growing in St. Louis (Jensen, 1912).

To determine the present occurrence of persimmon in the St. Louis area, a reconnaissance was made along the main highways radiating from the city. Although every side road could not be followed, and doubtless, in the forced pace of highway traffic, some trees were overlooked, a fairly complete idea of its local behavior was obtained. Figure 2 and Table II summarize the data obtained. It can be seen that persimmon does not occur within the city limits, and is primarily an upland tree which prefers an open drained habitat. Diospyros virginiana was usually found growing in clones or scattered in open situations where there is little competition; or else it was found scattered with other second growth trees or in young mixed-oak forests (pls. 25 and 26). In the former instance, the trees were young and were initiating growth, while in the latter instances they were comparatively old or dying and represented the last of their number. The present local absence of persimmon within the metropolitan area can not be explained on the basis of unfavorable habitat brought about by smoke or industrial gases, for trees are successfully grown as ornamentals in the city parks and at the Missouri Botanical Garden. Rather, the lack of dispersal agents for its seeds appears to be the underlying cause.

Persimmon is poorly equipped for dispersal by means other than animals, or, indirectly, by man. The fruit, a true berry, ranges from $\frac{3}{4}$ to $1\frac{1}{2}$ inches in diameter, and bears proportionately large seeds, four to eight in number. Once

separated from the pulp, the seeds are not light enough to be scattered by wind or to float upon water. In the city they can still be seen under cultivated trees, untouched by squirrels, rabbits, or rats, as late as June. Tables III and IV list the animals that eat persimmon fruits in the wild. Although these data do not show diet preferences, the fact that the animals listed do eat persimmon fruit indicates that they act in a large degree as dispersal agents for its seeds, since it is unlikely that the seeds are dispersed by any other means. In addition to the animals listed, the pine mouse will use the seeds as food (Martin, 1951), while the meadow mouse is known to include persimmon and *Bumelia* seeds among its caches, and thus figure in its dispersal (L. G. Brenner, personal communication, 1953). While certain birds eat the flesh or pulp of the fruit, it is doubtful whether any listed in Table III B (except the turkey now rare in Missouri) is able to swallow or void the large seeds. This is in contrast to sassafras (Sassafras albidum (Nutt.) Nees),

a "pioneer" species which does grow spontaneously within the city, whose fruit and seeds are eaten by birds and thus is scattered more widely than persimmon.

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TABLE III

LIST OF ANIMALS AND BIRDS EATING PERSIMMON FRUIT*

Spacios	Per cent of Diet	
opeeres	Southeast	Northeast
	A. ANIMALS	
Red Fox Gray Fox White-tailed Deer Opossum Raccoon Ring-tailed Cat (Texas only) Striped Skunk	$10-25 \\ 2-5 \\ 0.5-25 \\ 2-5 \\ 5-10 \\ 5-10 \\ 0.5-2$	0.5–2 0.5–2 Not recorded Not recorded 5–10
	B. Birds	
Wild Turkey Catbird Robin Yellow-bellied Sap-sucker Myrtle Warbler Cedar Waxwing Mockingbird	Not recorded 2–5 Not recorded 0.5–2 2–5 Not recorded	0.5-2 2-5 Not recorded Food item of undetermined extent 0.5-2 Not recorded Food item of undetermined extent

* Based upon stomach and crop analyses, droppings, and field observations (after Martin, 1951).

TABLE IV OCCURRENCE OF PERSIMMON IN MISSOURI WILDLIFE*

Species	Samples examined	Occurrence of persimmon
Deer	348 stomachs	40
Coyote	680 stomachs	51
Red Fox	731 stomachs	31
Gray Fox	251 stomachs	56
Quail	5,472 crops	33
Quail	1,358 droppings (roost)	1

* Prepared from letter, L. J. Korschgen, Missouri Conservation Commission, 1953.

HABITAT TYPES

As mentioned above, D. virginiana was found either initiating growth in abandoned places or as a minor element in mixed-oak associations. To interpret its behavior in these habitat types, data will be presented from sites where more complete studies were made.

Old Fields.—Many authors list D. virginiana as occurring in clones along roadsides, in old fields, and other waste places (Sargent, 1894; Eddy, 1927; Van Dersal, 1938; Steyermark, 1940). Personal observations were made along roadsides and in old fields at the Missouri Botanical Garden Arboretum, Gray Summit, where

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information concerning the history of the land is fairly complete. Here, three patterns of "field invasion" were found to be present. These may be characterized as:

- (1) Clonal: trees of varying ages, all of the same sex.
- (2) Clonal: trees of almost the same age, all of the same sex.
- (3) Scattered: trees of varying ages, both sexes present.

(1). A group of the first type was found in a sloping field, abandoned since 1924, which, except for the eradication of elm, had been allowed to grow wild (A. P. Beilmann, personal communication, 1953). An apparently injured, double

trunked tree, near a shallow gully, was the oldest element present (c. 20 years). Growing in association with it were Andropogon virginicus, Allium sp., Panicum, sp., Aster sp., Solidago sp., young Juniperus virginiana, Cornus racemosa, and Parthenocissus sp. In somewhat elongated concentric arcs about the old tree were other persimmon trees of different ages, the younger ones being on the periphery, but more numerous down the slope (pl. 25). Trees old enough to bear fruit showed the single peduncles characteristic of pistillate trees. Upon digging near the bases of several older trees, long horizontal spreading roots³ connecting the older trees were found at a depth of a foot (pl. 25). Several roots were followed for their entire lengths and were found to branch repeatedly. These gave rise to several small trees, one of which is shown in pl. 25. The diameter of the root remained almost constant (3/4 inch) except near the tips, where normal growth occurred. There were no evidences of decay or separation of root branches; nor were the branches themselves chance root grafts. From observations of other sites similar to this one (Table II) it was noted that the advance of the younger trees is usually more rapid down the slope, probably due to the greater development of the root system in this direction, a consequence of gravitational influence or greater soil moisture. Although the aspect of this site was largely clonal, a few of the smaller trees may have been seedlings, since seeds collected here were found to be viable.

(2). The second group was observed along a roadside near an abandoned field of similar history to the one above, except for possible disturbances due to road repairs. Other species growing at this site included: *Rhus glabra*, *Symphoricarpus* orbiculatus, Rubus sp., Andropogon virginicus, and Rudbeckia sp., as well as a few very young Juniperus virginiana trees. The largest persimmon trees examined here were all essentially the same age (about 15 years). They exhibited the uniform growth characteristics and the same sex of trees vegetatively propagated from a common stock, yet no "parent" tree as in the above situation was present (pl. 26). These trees were also found to be connected by stolons, while some individuals had their own groups of younger trees about them. Seeds found at this location were also viable. It is conceivable that this situation was brought about as a result of the

³There are references to persimmons as "stoloniferous" (Sargent, 1894; c.f. also, Holm, 1909). However, a complete description of this condition was not found in the literature. The roots described here did not appear to differ in gross structure from the normal roots.

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roots of an older persimmon tree having been accidentally cut into pieces and distributed, so that groups similar to those of the first type were concentrated in this small area. That this is possible is demonstrated by a common horticultural practice in which cuttings of persimmon are made for propagative purposes and vigorous sprouts are obtained from them. Further, decapitated trees have been reported to send up root suckers within two months after being injured (Fletcher, 1915).

(3). On the top of the slope of the same field, but away from the road, a third pattern was found. Here trees of varying ages and forms were scattered in groups.

Most of the trees were from 15 to 25 years old, although some seedlings were also found. The trees were both staminate and pistillate, and occurred in sporadic groups over the field. Most groups were composed of two or more trees, although some lone trees were noted. Ecologically, this site is part of the "highway" system used by deer and other animals at the Arboretum (Beilmann, personal communication, 1953). The scattered, but grouped trees closely reflect the way seeds are dropped by animals. Yet it is difficult to account for their non-clonal habit. The most likely explanation is that none of the trees were ever injured to the extent that they began to sucker. No plowing had been done in this field for over 25 years and the trees were not planted out. Injury by cattle grazing (besides trampling) is speculative; there are reports that cattle will not browse persimmon leaves or twigs (presumably because of calcium oxalate crystals and tannins present-Deam, 1932; Van Dersal, 1938); however, they are known to eat the leaves when suitable forage is not available (Brenner, personal communication, 1953), and many wild animals are reported to eat the buds and leaves (Missouri Conservation Bulletin, 1940). Forest associations.-From observations at the Missouri Botanical Garden Arboretum and in the St. Louis area, persimmon was never found upon a river flood plain (Table II), nor were mature trees ever found in a pure stand. Persimmon is frequently mentioned in the literature as existing in pure stands and as reaching its greatest proportions in the basin of the Mississippi River and along the Wabash River Valley. Ridgway (1882, 1894) and Sargent (1894) are probably the uncited sources for these references. However, a more recent survey of the hardwoods growing in Louisiana listed persimmon as only a minor species in all the habitats in which it was found (Lentz, 1929; Hepting, 1936), while Miller and Tehon (1929) report that no persimmon trees as described by Ridgway are now known in the Wabash Valley. Evidently, persimmon was more of a dominant tree (as were others) in the primeval forest than it is in the second growth timber of today.

That D. virginiana is only a minor element in present-day associations is verified by other authors. In the Ozark and adjacent plains region, Steyermark (1940) found D. virginiana occurring as a pioneer element on dolomitic glades, as a temporary dominant on bald knobs and bare limestone areas, and, frequently,

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initiating oak-hickory associations on the acid substrata of the prairie. However, he did not list it as a member in the building of a flood plain climax, in associations where burning-over had recently taken place, or in drainage regions. Palmer (1921) did not mention D. virginiana as a conspicuous element of the flora of the Ozarks. Although Lentz lists the persimmon as growing in both the well- and poorly-drained bottomlands of northeastern and southern Louisiana, it was not mentioned as occurring in the Louisiana swamps or in lands subject to overflow. In the Carolinas, Eddy (1927) found it growing at the edge of alder swamps and on the coastal plain, but again, only as a minor or subdominant species. This evidence indicates the wide range of ecological situations in which D. virginiana is able to initiate growth; yet, because of its slow rate of growth, it is shaded out by faster-growing trees. Brenner (1942, 1952) made comprehensive observations of the mixed oak associations in his environmental and quadrat studies at the Gray Summit Arboretum. An example of the short duration of the persimmon in an open woodland can be found from data reported by Brenner from a quadrat staked out in an oak coppice in 1937. At that time, numerous persimmon and other heliophilous trees were keeping pace in growth with the white oaks, the dominant tree. Since then, the white oaks made considerable growth, with the result that, 15 years later, one-fourth of the persimmons were dead and the remaining ones were in poor condition.

SUMMARY

1. Although formerly members of the genus *Diospyros* ranged far to the north, the native persimmon now appears to be limited in its spread to the north by an annual temperature of 25° F., and to the west by rainfall of 30 inches annually. Within these limits, however, it appears uncommon in the area of the Wisconsin glaciation.

Supplementary chromosome counts from Missouri (three counties) and Arkansas (one county) are in agreement with previously recorded determinations.
 Local absence of D. virginiana is attributed to eradication of the trees that were present in what is now the city. Dispersal of seeds is largely through the activities of animals, and for this reason persimmon is not known as a pioneer species within urban limits.

Three types of "field invasion" by persimmon in abandoned places are described. The ability of the roots to sucker upon injury accounts for the dense clones often found in these situations, although non-clonal situations also exist.
 Although persimmon once was known to occur in pure, dense stands,

more recent reports indicate that this is now not the case. Throughout its range persimmon is reported as a minor species in older associations.

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EXPLANATION OF PLATE

PLATE 25

Diospyros virginiana L.

Fig. 1. Clonal type 1: Trees are of varying ages, and same sex.

Fig. 2. Portion of a "stoloniferous" root from the above situation showing its branching nature and one young tree attached to it. (Length of root approximately 6 feet.)

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PLATE 25



SKALLERUP-DIOSPYROS VIRGINIANA L.

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PLATE 26



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EXPLANATION OF PLATE

PLATE 26

Diospyros virginiana L.

Fig. 1. Clonal type 2: Trees are essentially the same age, and are of the same sex.

Fig. 2. Tree group characteristic of the third type. Fig. 3. Persimmon in mixed oak association.

